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# Phenological patterns of soil microarthropods from three climate regions

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**Abstract**

The phenological patterns of Acari and Collembola from three climate regions (Monsoon, Mediterranean and Temperate) were analysed by using a phenological model. The phenograms derived are compared on the grounds of certain parameters of the model. Phenograms of animals inhabiting the temperate region were not periodic but a pattern of periodic vertical movements is evident in the case of Collembola. In both the monsoon and the Mediterranean regions, the populations exhibit seasonal patterns of abundance oscillations following the seasonality of the climate. Differences between taxa as well as between regions are discussed.

**Keywords:** Phenology, model, microarthropods, monsoon, Mediterranean climate.

*Patterns phénologiques pour les microarthropodes du sol de trois régions climatiques.*

**Résumé**

Les patterns phénologiques pour les Acariens et les Collemboles de trois régions climatiques (à mousson, méditerranéenne et tempérée) ont été analysées en utilisant un modèle phénologique. Les phénogrammes dérivés sont comparés sur la base de certains paramètres du modèle. Les phénogrammes pour les animaux vivant dans la région tempérée ne sont pas périodiques, mais un pattern de déplacements verticaux périodiques est évident chez les Collemboles. Dans les deux autres régions, à mousson et méditerranéenne, les populations montrent des patterns saisonniers d'oscillations d'abondance en rapport avec la saisonnalité du climat. Des différences entre taxons, comme entre régions, sont discutées.

**Mots-clés :** Phénologie, modèle, microarthropodes, mousson, climat méditerranéen.

## INTRODUCTION

Phenology reflects certain aspects of the demography of a population, that is the timing of its life cycle characteristics in a given environment. Although the phenological patterns of soil microarthropod populations may appear quite complex, hypotheses regarding their life cycle strategies can be formulated on the grounds of phenological data (Mitchell, 1977; Luxton, 1981; Stamou and Sgardelis, 1989; among others). Thus, various attempts have been made to classify phenological patterns of soil microarthropods into categories or types (*see* Lebrun, 1971; Wolda, 1988). Such an attempt is better undertaken by using phenological models (Van Straalen, 1982; Stamou and Sgardelis, 1989; Stamou *et al.*, 1993).

In this paper we consider the skewness of phenograms of soil microarthropod populations from three climate regions: Monsoon, Mediterranean and Temperate. We try to interpret the asymmetries of the phenograms associated with the timing of the life cycle of soil microarthropods.

## MATERIAL AND METHODS

The data originate from a range of climate regions, i.e. monsoon-type (Northeastern India), semiarid Mediterranean (Southern Greece), sub-humid Mediterranean (Northern Greece) and Temperate (France). Details regarding the sites and the sampling procedures are given in Sarkar (1990), Sgardelis and Margaris (1993), Asikidis and Stamou (1991) and Athias-Henriot and Cancela da Fonseca (1976) respectively. Ombrothermic data for the studied sites and periods are shown in figure 1.

The phenological model proposed by Stamou *et al.* (1993) was used for the description of the phenology of the populations. In this model it is assumed that the phenology of any population inhabiting a seasonal environment can be described by a symmetric periodic curve:

$$f(\mathrm{ET}) = \mathrm{EXP}\,(a + b \cdot \mathrm{COS}\,(2 \cdot \pi \cdot (\mathrm{ET} - \varphi)/\mathrm{T})) \qquad (1)$$

where the independent variable ET, termed Ecological time, is a periodic function of standard clock time (ST), ET = f(ST). In the course of standard time, Ecological time is going faster during periods of sharp changes in abundance and slower during periods of abundance stability. Thus, the proposed equation describing the length of the Ecological time unit ($\Delta_{ET}$) as a function of Standard time ST is:

$$\Delta_{\mathrm{ET}} = f(\mathrm{ST}) = \mathrm{EXP}\,(a_1 + b_1 \cdot \mathrm{COS}\,(2 \cdot \pi \cdot (\mathrm{ST} - \varphi_1)/\mathrm{T}_1)) \qquad (2)$$

The model has eight parameters of which the period T and the phase $\varphi$ of the phenogram, as well as period $T_1$ and the phase $\varphi_1$ of the function relating ET to ST, are the most important. The period T and the phase $\varphi$ of the phenograms are expressed formally in ET units. For convenience they could be expressed in ST units (as T' and $\varphi$') by using equation (2) for the calculation of the Standard time T' or $\varphi$' which corresponds to T or $\varphi$ units in the Ecological time-scale (*see* Stamou *et al.*, 1993; fig. 1). The phase difference $\Delta\varphi = \varphi' - \varphi_1$ is of special importance since it is responsible for the

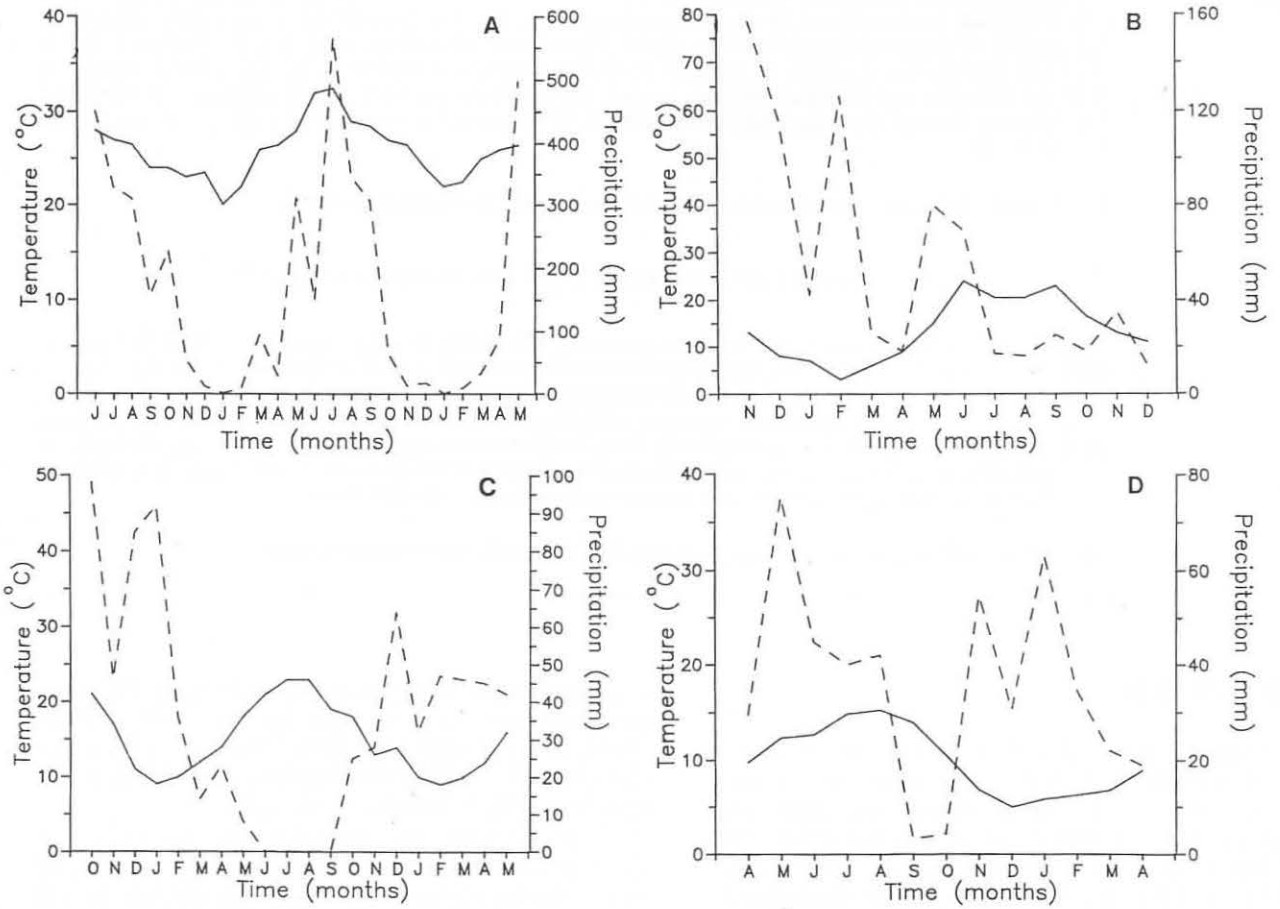
A
B
C
D
Temperature (°C)
Precipitation (mm)
Time (months)
J J A S O N D J F M A M J J A S O N D J F M A M
N D J F M A M J J A S O N D
O N D J F M A M J J A S O N D J F M A M
A M J J A S O N D J F M A

**Figure 1.** - Temporal variations of temperature (Solid line) and precipitation (Dashed line) in the four regions studied: *a*) Monsoon (India). *b*) Subhumid Mediterranean (Northern Greece). *c*) Semiarid Mediterranean (Southern Greece). *d*) Temperate (France).

type of the skewness of the phenograms. For $\Delta\varphi > 0$, the highest rate of demographic events coincides with the period of increasing population density, resulting in right-skewed phenograms, while for $\Delta\varphi < 0$, the highest rate of demographic events coincides with the period of decreasing population density, resulting in left-skewed phenograms. Finally, for $\Delta\varphi = 0$ the phenogram will be symmetric. It is to be noted, however, that the degree of skewness depends on the value of the parameter bl. If bl=0 the Ecological time unit is of constant length and the phenogram is symmetric regardless of the phase difference. For the comparison of phenograms two more parameters can be derived. a) An estimation of the sharpness (curtosis) of the phenogram $C=(R_2-R_1)/T'$, where $(R_2-R_1)$ is the time interval around the phase $\varphi'$, during which the abundance is above overall mean, and b) an estimation of the skewness of the phenogram $S=(\varphi'-\varphi_m)/T'$ where $\varphi_m$ is the time (in ST units) when the abundance of the population is at minimum. Thus, phenograms displaying a peak at $\varphi'-\varphi_m=T'/2$ (half period) would be symmetric (S=0.5), phenograms displaying a peak soon after the minimum (S<0.5) would be right skewed, and phenograms with S>0.5 would be left skewed. The model was fitted on log-transformed census data. For $ET_i=f(ST_i)$ given as a time vector and for a given set of $\varphi$ and T, the parameters a and b were estimated by least-square regression.

## RESULTS

### Phenology of Cryptostigmata, Gamasida and Collembola

Seasonal variations in Cryptostigmata, Gamasida and Collembola abundance in the monsoon region (India) and the dry and humid Mediterranean ones (Greece) are shown in figure 2. In figure 3 are shown the phenograms of Collembola sampled at different soil layers of the temperate forest in France. The parameters T', $T_1$, $\varphi'$ and $\varphi_1$ of the fitted phenological model and the values of $\varphi_m$, $\Delta\varphi$ and S are given in table I.

There were no obvious seasonal trends of abundance variations of soil microarthropods in the temperate forest and the phenological model failed to fit the data. The abundance of both mites and Collembola (not plotted) fluctuates almost randomly throughout the year. In the monsoon and the Mediterranean regions mites and Collembola exhibited a clear seasonal trend with period T' varying between 11.3 and 17 months (table I). In both regions, Cryptostigmata exhibit a right-skewed phenological pattern. Their abundance increased rapidly soon after the adverse period (monsoon in India, summer drought in Greece) was over and rose to a peak during late autumn ($\varphi'=6.6$) in India and early winter ($\varphi'=3.1$) in Greece. The decline of their abundance was gradual and occurred during spring in both regions. The abundance

**Table I.** -The estimated parameters T', $\varphi'$, $T_1$ and $\varphi_1$ of the fitted model in standard time units (months). $\Delta\varphi$ is the phase difference $\varphi' - \varphi_1$ in months, $\varphi_m$ denotes the time in standard time units when the abundance was minimum and $S = (\varphi' = \varphi_m)/T'$ is the skewness index.

| Region/taxon | T' | $\varphi'$ | $T_1$ | $\varphi_1$ | $\Delta\varphi$ | $\varphi_m$ | S |
|---|---|---|---|---|---|---|---|
| *Monsoon:* | | | | | | | |
| Collembola | 12.2 | 6.8 | 9.0 | 6.5 | 0.3 | 0.7 | 0.50 |
| Cryptostigmata | 12.0 | 6.6 | 11.4 | 4.6 | 2.0 | 2.4 | 0.35 |
| Gamasida | 12.0 | 7.5 | 11.1 | 10.9 | -3.4 | 0.8 | 0.56 |
| *S. caprai* | 12.4 | 6.9 | 11.9 | 5.5 | 1.4 | 2.3 | 0.37 |
| *S. rectus* | 12.2 | 7.1 | 11.9 | 5.9 | 1.2 | 2.3 | 0.39 |
| *S. striatus* | 11.8 | 7.8 | 11.2 | 2.3 | 5.6 | 1.9 | 0.50 |
| *Semiarid Mediterranean:* | | | | | | | |
| Collembola | 13.6 | 5.3 | 15.9 | 10.2 | -4.9 | -3.3 | 0.63 |
| Cryptostigmata | 13.4 | 3.1 | 9.2 | 1.3 | 1.8 | -0.7 | 0.28 |
| Gamasida | 17.0 | 5.4 | 16.0 | 8.3 | -2.9 | -4.6 | 0.59 |
| *Sub-humid Mediterranean:* | | | | | | | |
| Collembola | 11.6 | 6.3 | 13.1 | 9.2 | -2.9 | -1.5 | 0.67 |
| Cryptostigmata | 11.9 | 3.1 | 11.7 | 0.9 | 2.2 | -1.3 | 0.37 |
| Gamasida | 11.3 | 4.8 | 11.4 | 9.6 | -4.8 | -1.2 | 0.53 |
| *S.* cf *latipes* | | | | | | | |
| Adults | 12.5 | 2.6 | 12.2 | 2.8 | -0.2 | -7.9 | 0.84 |
| Eggs/Female | 13.8 | 6.9 | 13.0 | 10.1 | -3.2 | -1.9 | 0.64 |
| Larvae | 14.2 | 8.0 | 14.0 | 7.2 | 0.8 | 1.7 | 0.43 |
| Protonymphs | 14.0 | 8.5 | 12.6 | 7.2 | 1.3 | 5.4 | 0.22 |
| Deutonymphs | 13.8 | 8.8 | 15.2 | 6.6 | 2.2 | 5.4 | 0.25 |
| Tritonymphs | 11.0 | 10.6 | 13.0 | 6.8 | 3.6 | 6.0 | 0.42 |
| *Temperate:* | | | | | | | |
| F0 layer | 12.0 | 4.5 | 10.0 | 5.6 | -2.8 | -4.1 | 0.72 |
| F1 layer | 9.4 | 3.2 | 11.3 | 5.6 | -1.0 | -3.4 | 0.70 |
| M0 layer | 9.6 | 5.7 | 12.5 | 3.2 | 1.2 | 2.8 | 0.30 |
| M1 layer | 10.6 | 7.4 | 12.5 | 4.1 | 1.1 | 3.5 | 0.37 |

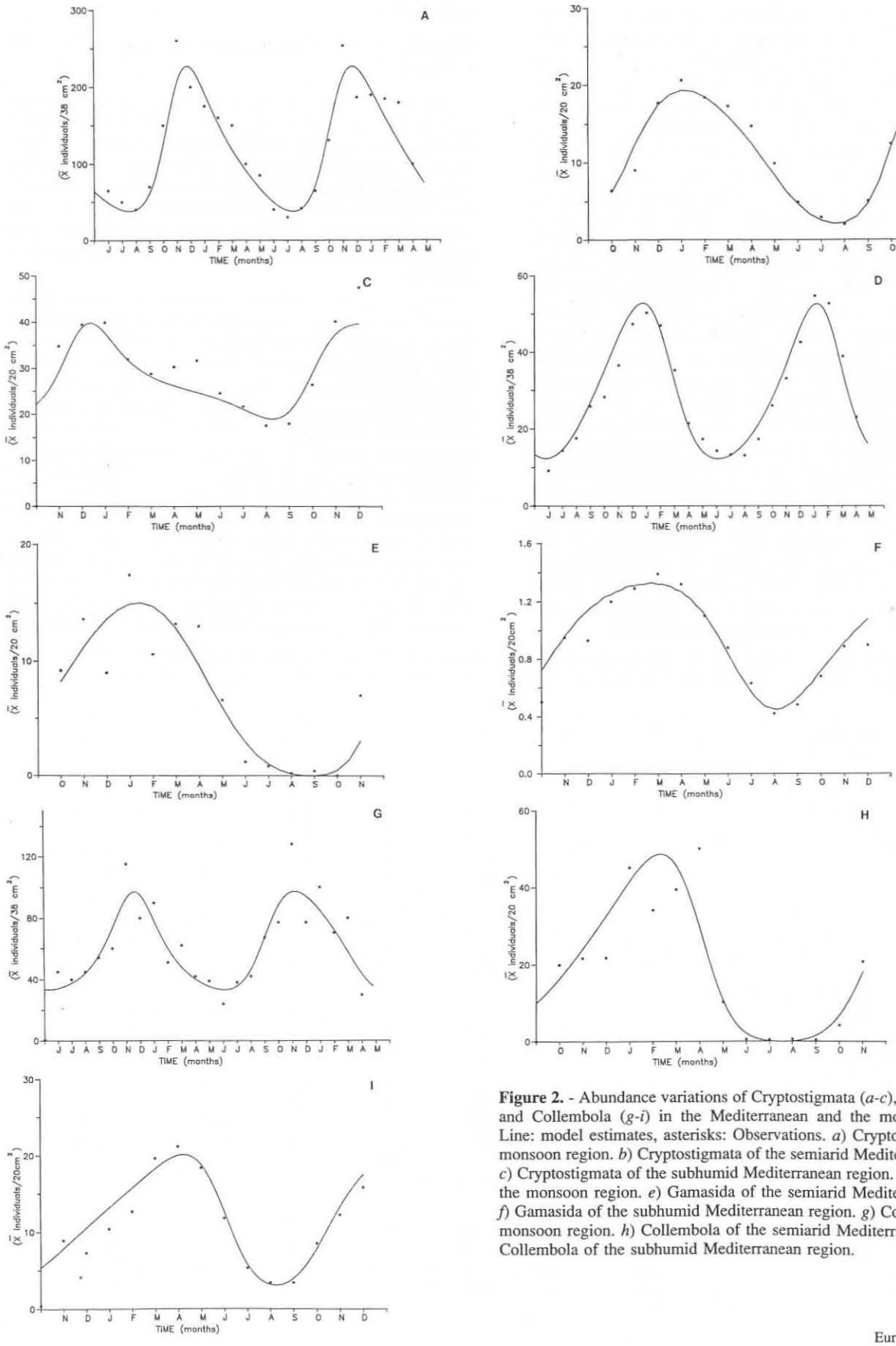


**Figure 2.** - Abundance variations of Cryptostigmata (*a-c*), Gamasida (*d-f*) and Collembola (*g-i*) in the Mediterranean and the monsoon regions. Line: model estimates, asterisks: Observations. *a*) Cryptostigmata of the monsoon region. *b*) Cryptostigmata of the semiarid Mediterranean region. *c*) Cryptostigmata of the subhumid Mediterranean region. *d*) Gamasida of the monsoon region. *e*) Gamasida of the semiarid Mediterranean region. *f*) Gamasida of the subhumid Mediterranean region. *g*) Collembola of the monsoon region. *h*) Collembola of the semiarid Mediterranean region. *i*) Collembola of the subhumid Mediterranean region.

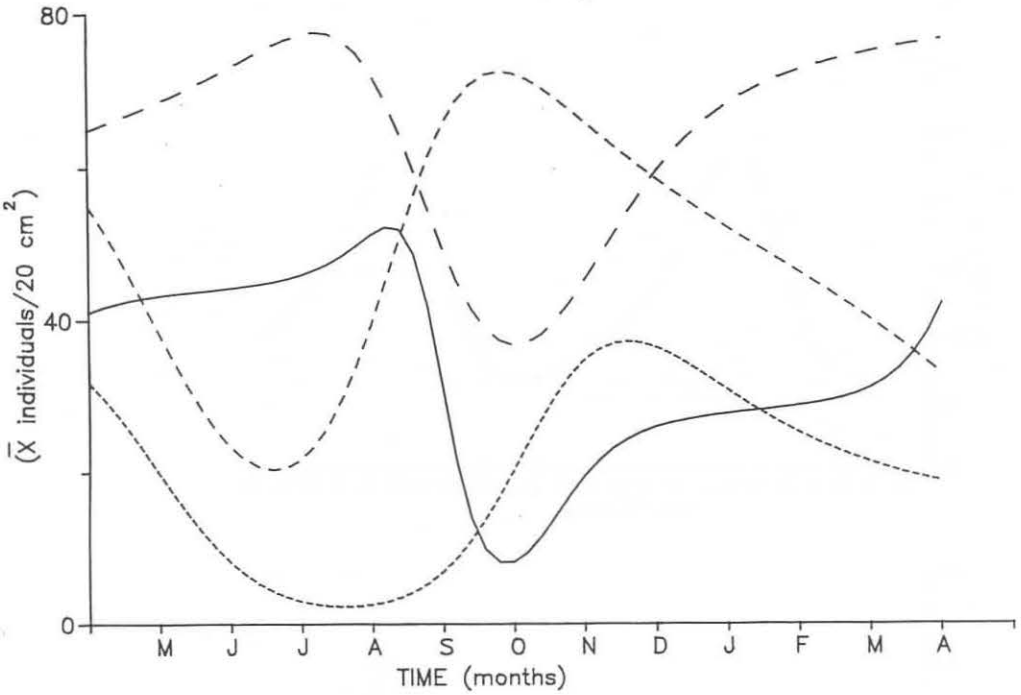


**Figure 3.** - Model estimations for the temporal variation of Collembola abundance in different soil layers of the temperate forest (Fontainebleau, France). Solid line: Abundance of Collembola in the F0 layer. Large dash: Abundance of Collembola in the F1 layer. Short dash: Abundance of Collembola in the M0 layer. Points: Abundance of Collembola in the M1 layer.

of Collembola exhibited right-skewed phenology in the monsoon region and left-skewed phenology in the Mediterranean one. In the monsoon region, their phenology followed closely that of Cryptostigmata. In the Mediterranean region the abundance of Collembola increased gradually after drought to attain peak density during spring and decreased rapidly afterwards. Finally, the abundance of Gamasida exhibited right-skewed phenology in both regions.

In the temperate region, despite the aseasonal variation of the abundance of Collembola, there was a certain pattern of seasonal vertical movements (fig. 3). It seems that Collembola migrates towards the mineral layers during summer and towards the organic layers afterwards.

## Phenology of *Scheloribates* spp. of India and Greece

Species of the genus *Scheloribates* are among the dominant ones in both the monsoon and the Mediterranean regions (Asikidis and Stamou, 1991; Sarkar, 1990). In the monsoon region, adult *S. caprai* (fig. 4a) and *S. rectus* (fig. 4b) exhibited the same phenological pattern, similar to that of the whole of the Cryptostigmata. This is not the case for *S. striatus* (fig. 4c) whose phenogram is right skewed and almost flat. In Northern Greece, the adults of *S.* cf. *latipes* displayed a sharp density peak in early autumn (fig. 5a). Afterwards, its abundance remained low and almost stable. Eggs first appeared during autumn and were carried in the abdomen of females until early summer. The ontogenetic development from egg to adult occurred during summer (fig. 5) and was a rather rapid process leading to the sharp increase of the abundance of matures soon after the drought period was over.

## Classification of the phenograms

Using the phenological model, complex phenograms can be classified into types considering their skewness, curtosis, phase and period. In all the cases studied the period is about 12 months. A simple ordination of phenograms can be obtained by using the sharpness index C and the skewness index S (fig. 6ab). The phenograms of Acari and Collembola are grouped into three main categories (fig. 6a), i.e. left-skewed leptocurtic (mostly Cryptostigmata), right-skewed platycurtic (Gamasida from Greece and *S. striatus* from India) and right-skewed leptocurtic (Collembola from the Mediterranean region and Gamasida from India). There were no left-platycurtic phenograms. The phenograms of different stadia of the life cycle of *S.* cf. *latipes* are grouped into two types (fig. 6b), i.e. left-skewed leptocurtic (juveniles) and right-skewed leptocurtic (adults and eggs carried in the abdomen of females). Although all phenograms are leptocurtic there are differences in the curtosis scale. Adults and early stadia exhibit more sharp-pointed phenograms than later stadia and eggs.

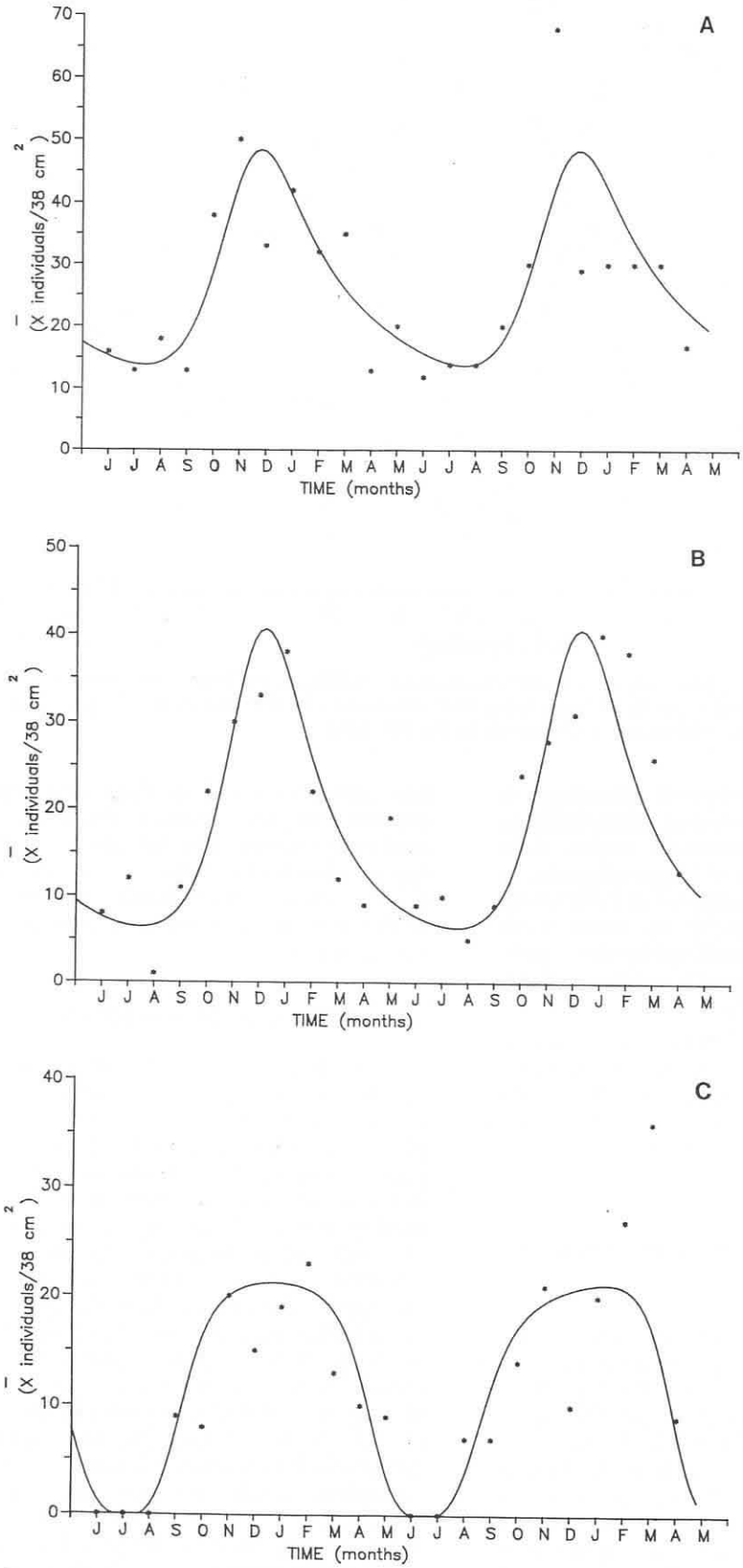


**Figure 4.** - Model estimations (solid line) of the observed (asterisks) temporal variation of abundance of *a*) *Scheloribates caprai* *b*) *S. rectus* and *c*) *S. striatus* from India.

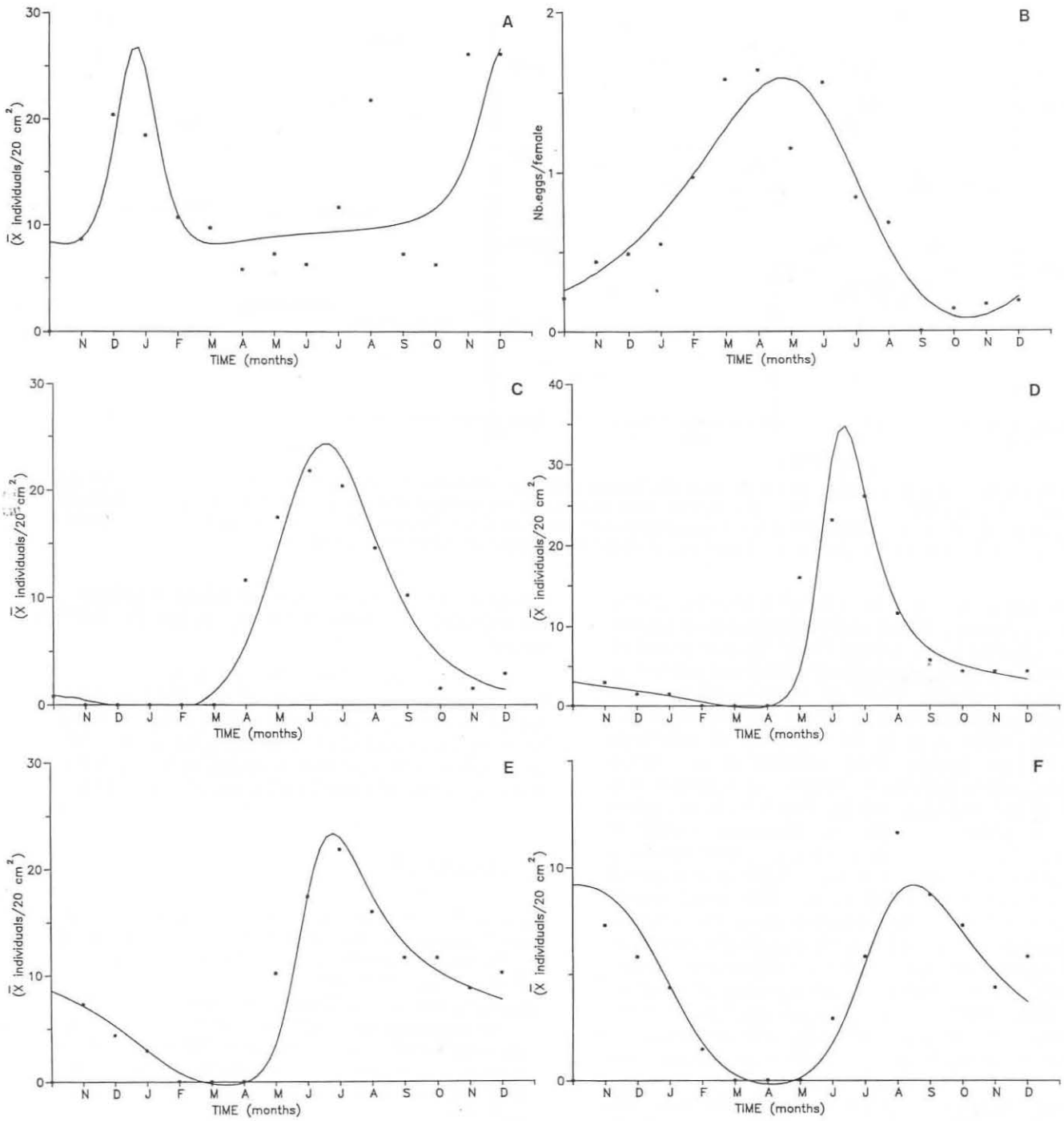


**Figure 5.** - Temporal variations of abundance of Scheloribates cf. latipes life stages. *a*) Adults, *b*) Eggs/female, *c*) Larvae, *d*) Protonymphs, *e*) Deutonymphs and *f*) Tritonymphs. Line: Model estimates, asterisks: Observations.

## DISCUSSION

Soil microarthropods inhabiting seasonal environments such as the monsoon and the Mediterranean ones studied in India and Greece, can encounter seasonality by adjusting the timing of their life-cycle development. On the contrary, populations of at least Collembola living in a temperate region such as Fontainebleau seem to overcome abiotic variation by migrating through the soil layers. Thus, the response of populations to strongly seasonal environments can be described rather on the temporal scale than on the vertical dimension of the spatial scale. The inverse happens with populations living in

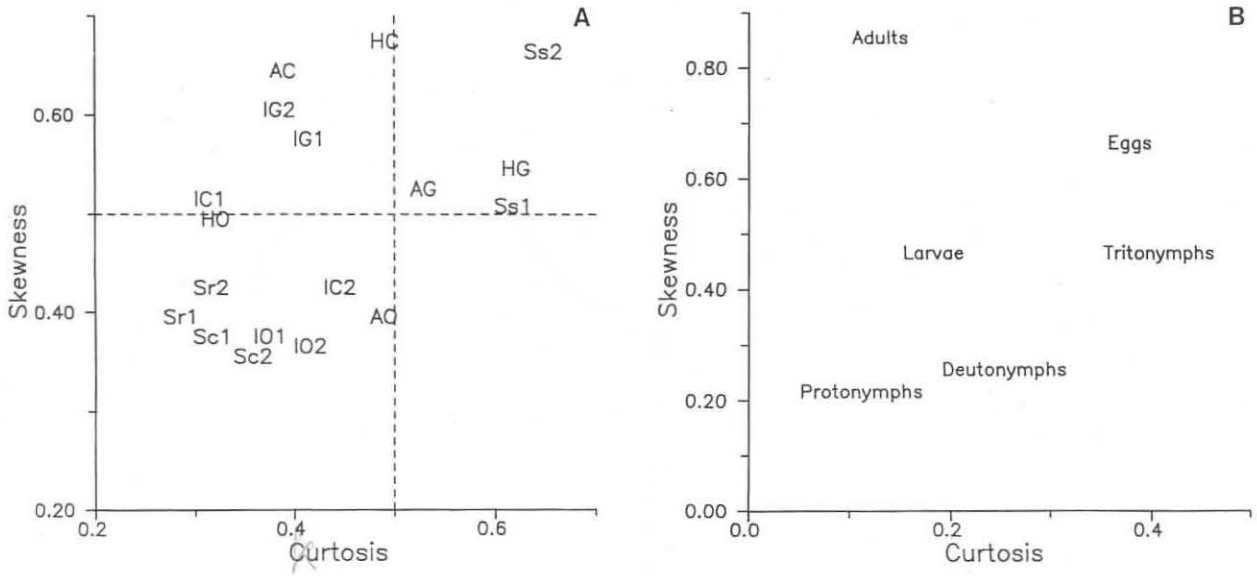


**Figure 6.** - Ordination of phenograms into the skewness (S) - curtosis (C) plane. (Skewness: left skewed < 0.5; right skewed > 0.5 Curtosis: leptocurtic < 0.5; platycurtic > 0.5). *a*) Mites and Collembola from the monsoon and the Mediterranean regions. Codes I = India, A = Semiarid Mediterranean, H = Subhumid Mediterranean, O = Cryptostigmata, G = Gamasida, C = Collembosa, Sc = *Scheloribates caprai*, Sr = *S. rectus*, Ss = *S. striatus*, 1 = first year of study and 2 second year of study. *b*) Life stages of *Scheloribates* cf. *latipes*.

less seasonal environments (*see* also Kaneko, 1985). In the monsoon as well as in the Mediterranean region, soil microarthropods respond to the adverse period of the year by displaying asymmetric seasonal patterns of abundance variation. There are taxon-specific as well as region-specific patterns of abundance variations reflecting differences in the strategies of avoidance or tolerance against stress (Stamou *et al.*, 1993). Cryptostigmata appears to respond in a similar way in both the monsoon and the Mediterranean regions and the same holds for the dominant species of *Scheloribates* but *S. striatus*. They are characterized by low abundance during the onset of the adverse period and a rapid development of juveniles which occurs either during the adverse period (Greece) or soon after (India). Gamasida, exhibit right-skewed phenograms in both regions. However, there are differences between phenograms of different regions regarding the curtosis. The phenograms of Gamasida are platycurtic in the Mediterranean region, where they seem to tolerate the effects of drought, and leptocurtic in the monsoon one. Finally, considerable differences in phenology between regions are exhibited by Collembola. The right-skewed phenology of Collembola in the monsoon region is possibly due to a rapid development of juveniles of the dominant species soon after the monsoon or due to massive upward vertical migration of individuals living in deeper soil layers during the monsoon. The left-skewed phenology of Collembola in the Mediterranean region can be attributed to high mortality rates at the onset of the drought followed by a succession of species with different phenologies during the rainy season (Argyropoulou, *in prep.*). At the onset of the drought period most Collembola seem to lay large numbers of eggs before dying (*see* also Poinsot-Balaguer, 1976). Therefore Collembola populations are expected to develop from eggs during the rainy season.

To sum up, in regions with strong seasonal, and thus predictable, oscillations of the environmental variables, the response of soil microarthropods could be exemplified mainly on a demographic basis, while in a region with smoother seasonal oscillations this response is linked rather to their vertical movements.

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